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Tropical Estuarine Angiosperm vegetation in the Neogene sediments of Bhutan, Eastern Himalaya, and remarks on Palaeogeography of Siwalik foreland basins of Indian Subcontinent

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Abstract

Impression–compression angiosperm leaf remains and rich palynoflora from Neogene sediments of Bhutan, Eastern Himalaya, expose a predominantly tropical-subtropical, humid vegetation with high rate of precipitation. Angiosperm floristic of mild coastal environment initiated during Formation I (Lower Siwalik). Diverse angiosperm vegetation including estuarine mangrove forest flourished in the area in the upper part of Lower Siwalik and basal part of Formation II (Middle Siwalik). Coastal environment gradually receded in Formation III (Upper Siwalik). Temperate climate angiosperm plant representatives are encountered in the Middle Siwalik with inconspicuous diversity and frequency which increase slightly in the Upper Siwalik.

Geographical position of Bhutan, Eastern Himalaya, was towards more lower latitude and enjoying tropical climate, higher rate of precipitation and marine inundation during Neogene period. Orogenic movements of Himalayan upliftment have changed the nearshore palacogeography of the area towards a highland mountainous topography since Late Upper Siwalik.

Tropical-subtropical environment prevailed in the other Siwalik foreland basins of Indian Subcontinent and mangrove esturine forest thrived in Himachal Pradesh sector during Late Lower Siwalik. More influence of temperate plant pollen in the Lower, Middle and Upper Siwalik in the western sectors suggest more early and active orogenesis in the areas compared to Eastern Himalaya.

INTRODUCTION

Angiosperm fossils are recorded from Neogene sediments of each of the seven Siwalik sectors (Fig. 1) of Indian subcontinent in the form of impression, compression of leaf, fruit, seed or petrified wood by various workers after the pioneering contribution of Sahni (1931). Extensive palynological study of Siwalik sediments has exposed a rich angiosperm vegetation of variable environment.

Plant megafossil and palynological studies of the Neogene sediments of Bhutan (Ban-

erjee, 1984, 1985, 1991, 1995; Banerjee & Das Gupta, 1984, 1995; Das Gupta, 1991) have accumulated enormous data to interpret the environment and palaeogeography of the Siwalik succession in Eastern Himalaya.

Modern angiosperm flora of Bhutan, Eastern Himalaya

The Himalayan foot hills of Bhutan included in the sub-tropical rain forest zone exhibit a thick luxurious vegetation. At higher elevations between 1800-3000 m a moist temperate flora flourish. Fifty six angiosperm families are recorded from Bhutan and Sikkim by Grierson and Long (1983, 1984). The families are Myricaceae, Juglandaceae, Salicaceae, Betulaceae, Fagaceae, Ulmaceae, Moraceae, Urticaceae, Cannabaceae, Proteaceae, Olacaceae, Opiliaceae, Santalaceae, Loranthaceae, Balanophoraceae, Polygonaceae, Phytolaccaceae, Nyctaginaceae, Aizoaceae, Portulacaceae, Basellaceae, Caryophyllaceae, Chenopodiaceae, Amaranthaceae, Cactaceae, Magnoliaceae, Annonaceae, Myristicaceae, Schisandraceae, Illiciaceae, Lauraceae, Tetracentraceae, Eupteleaceae, Ranunculaceae, Circaeasteraceae, Berberidaceae, Podophyllaceae, Lardizabalaceae, Menispermaceae, Nymphaeaceae, Saururaceae, Piperaceae, Chloranthaceae, Aristolochiaceae, Dilleniaceae, Actinidiaceae, Dipterocarpaceae, Theaceae, Clusiaceae, Hypericaceae, Droseraceae, Fumariaceae, Papaveraceae, Capparaceae, Brassicaceae and Moringaceae. In addition, Biswas et al. (1976) in unpublished ONGC report have mentioned about occurrence of some more families. Among these families Dipterocarpaceae *(Shorea robusta)*, Magnoliaceae *(Michelia chambelli)*, Dilleniaceae *(Dillenia pentagyna, D. indica)*, Theaceace *(Schima wallichii)*, Sterculiaceae *(Sterculia villosa)*, Bombacaceae *(Salmolia malabaricum)*, Lythraceae *(Lagerstroemia oblatum)*, Combretaceae *(Terminalia bellerica)*, Bignoniaceae *(Stereospermum chelonoides)* are common.

Geology of the Neogene sediments of Bhutan Siwalik sector

Neogene sedimentary successions exposed in East Bhutan, Eastern Himilaya, have been recognised by Biswas et al. (1979) as Formation I, Formation II, Formation III and Diklai Conglomerate and correlated with the Western Siwalik sediments. The latest proposition of correlation by Acharyya (1994) is enumerated below from younger to older sequence :

Neogene (Miocene)	Formation III	Upper Siwalik
	Formation II	Middle Siwalik
	Formation I	Lower Siwalik

The Diklai Conglomerate is suggested to be a post Siwalik Quaternary deposition.

Angiosperm floristics of Siwalik sediments of Bhutan

Angiosperm floristic study of Bhutan Siwaliks has been made with samples of four river traverses (Fig. 1). Megaplants are from the angiosperm leaf bearing beds of basal part of

Tropical estuarine Angiosperm vegetation in the Neogene sediments of Bhutan

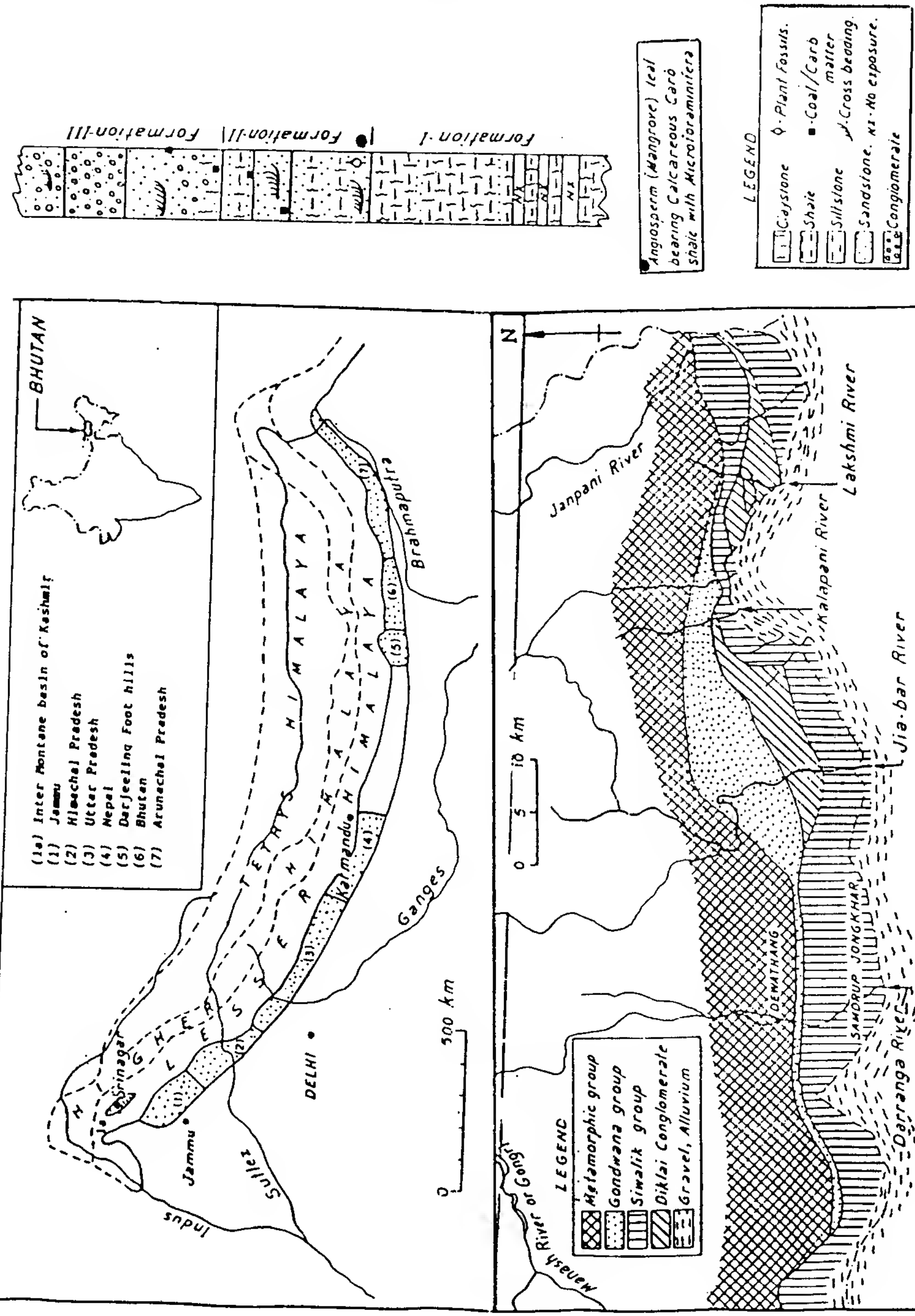

Fig. 1. Map of Indian subcontinent, seven Siwalik sectors and four river traverses in East Bhutan; lithosuccession of Siwalik sediments of Bhutan (After Biswas et al., 1979).

Middle Siwalik. Palynoassemblages are recovered from samples of Lower, Middle and Upper Siwalik (Fig. 1).

Angiosperm leaf remains from Bhutan

Thorough external and internal morphographic studies of angiosperm leaf remains have recognised a floral assemblage of predominantly tropical, subtropical climate. The carbon layer preserved on some of the leaves have recovered cuticular layers. The cuticular structures have revealed characteristics of mangrove plants of estuarine habitat. The following angiosperm plants are identified from the basal part of Middle Siwalik of Bhutan (Fig. 2).

Table 1

Angiosperm leaf (Dicotyledons)	Affinity	Environment
Darrangiophyllum ellipticum Banerjee & Das Gupta, 1984 emend. Banerjee, 1991, 1995	cf. *Aegiceras* sp. Myrsinaceae	Tropical humid, Estuarine
Dicheria ellipticalis Banerjee & Das Gupta, 1984	Uncertain	Tropical sub-tropical humid
Ghosia sp. Banerjee & Das Gupta, 1984	Uncertain	Tropical humid
Pseudopaxillatophyllum sp. Banerjee & Das Gupta, 1984	Clusiaceae/? Aegialitidaceae	Tropical humid ? Estuarine
Siwalikiphyllum acuminatum Banerjee & Das Gupta, 1984 emend Banerjee, 1991, 1995	cf. *Avecinnia* sp. Avecinniaceae	Tropical humid, Estuarine

Explanation of Fig. 2. A. *Darrangiophyllum ellipticum* (Nos. I–V) [Sp. No. BH/31], *Siwalikiphyllum acuminatum* (Nos. VI – VIII); B. Shows 1°, 2°, 3° veins and forking of 4° veins within the areoles [Sp. No. BH/31 (No. 1)] ; C. Cuticular layer of *Darrangiophyllum ellipticum* with irregularly distributed crowded *Heliospermopsis darrangei* [Sp. No. BH/31(2)]; D. Cuticular layer of *Siwalikiphyllum acuminatum* with *Heliospermopsis siwalikii* in linear rows. [Sp. No. BH/31 (21)] I; E. *Siwalikiphyllum acuminatum* ; F. *Dilcheria ellipticalis;* G. *Ghosia furcata;* H. *Pseudopaxillatophyllum ellipticum;* I. *Darrangiophyllum ellipticum;* J. *Darrangiophyllum elongatum;* K. *Darrangiophyllum auriculatum.*

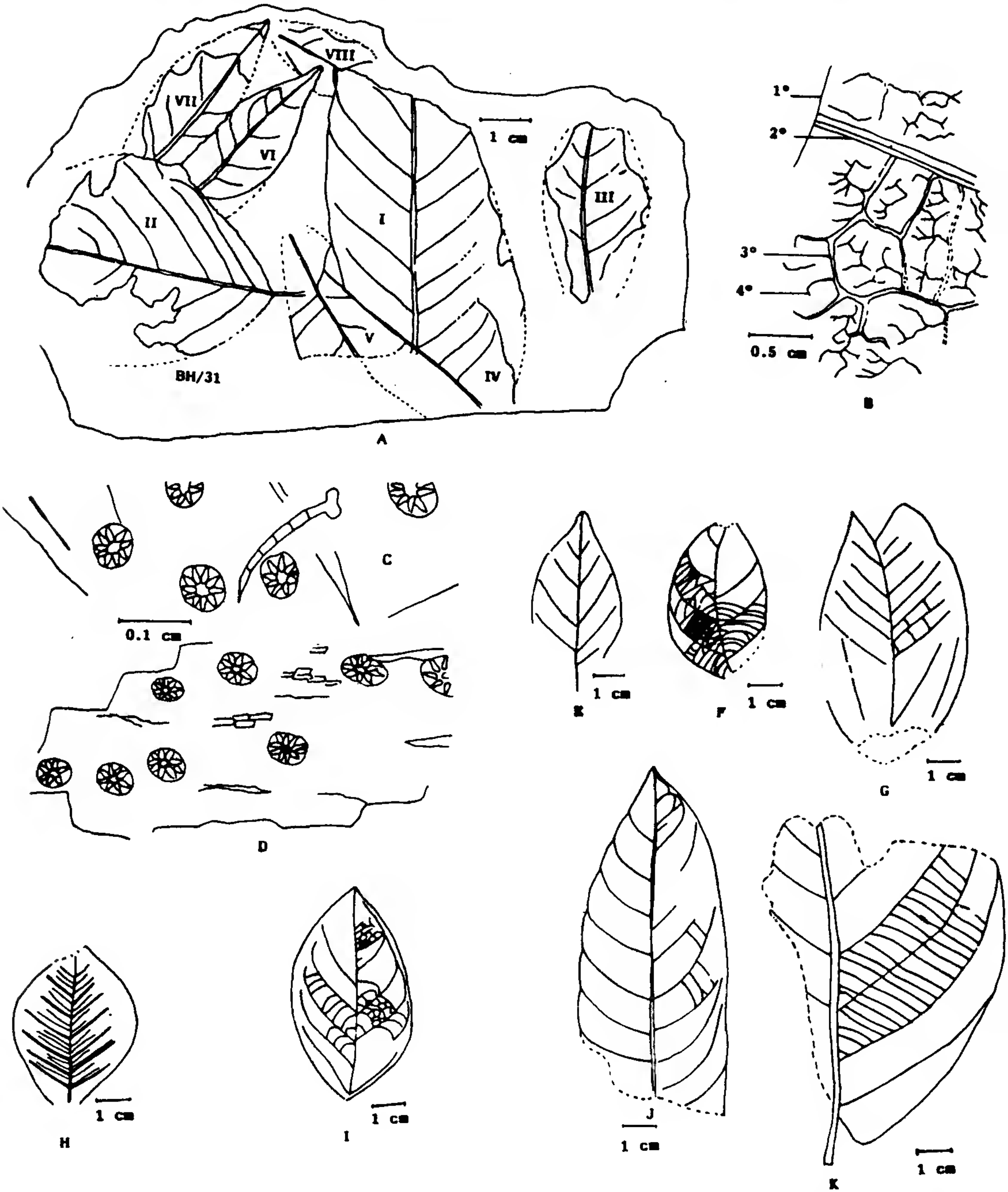

Fig. 2. Angiosperm leaves from Siwalik sediments of Bhutan: details of venation pattern of the leaves, and deatils of cuticular structures recovered from the compression specimens.

Diagnoses of *Darrangiophyllum ellipticum* and *Siwalikiphyllum acuminatum* (Banerjee & Das Gupta, 1984) have been emended with the additional observations made through cuticular study of the leaves showing crowded glandular trichomes (Banerjee, 1984, 1985, 1991, 1995). The glandular trichomes cf. salt glands of mangrove plant leaves are recovered in dispersed condition in the Tertiary palynoassemblages along with shallow marine microplankton. The isolated trichomes were named as *Heliospermopsis* by Nagy (1965) from Hungary and *Oudhkusumites* by Srivastava (1967) from India; the latter is now considered as a synonym of *Heliospermopsis* Nagy and the species considered under new combination (Banerjee, 1991, 1995). *Heliospermopsis* in dispersed condition and for the first time *in situ* in the cuticles of extinct angiosperm leaves were described from Darjeeling foot hills and Bhutan (Banerjee, 1984, 1985); identifiaction of *Heliospermopsis* as salt glands of mangrove plant leaf cuticles has been made through comparative study of extant leaf cuticles including mangrove plant *Aegiceras* spp., *Avecinnia* spp. and others (Banerjee, 1984, 1985). Brief descriptions of *Siwalikiphyllum acuminatum* and *Darrangiophyllum ellipticum* are provided below.

Siwalikiphyllum acuminatum Banerjee et Das Gupta (1984), emend. Banerjee, 1991, 1995.

Lamina nannophyllous, margin entire, narrowly elliptic, apex acuminate, venation pinnate, primary (1°) vein stout, straight, 2° veins alternate to opposite, camptodromous, ? brochiodromous, 3° veins indistinct with faint reticulation. Cuticles of both the layers with indistinct epidermal cells are crowded with multicellular glandular trichome *Heliospermopsis siwalikii* Banerjee (1995). The trichomes are arranged in linear rows; frequency of occurrence is 21–32/mm^2 (Fig. 2).

Darrangiophyllum ellipticum Banerjee et Das Gupta (1984), emend. Banerjee, 1991, 1995.

Lamina microphyllous, margin entire, narrowly ovate, apex obtusely acute , base obtuse cuneate, venation pinnate, 1° vein stout, straight, 2° veins eucamptodromous, 3° veins distinct, emerge at right angle from 1° or 2° veins, reticulation conspicuous, rectangular to polygonal in shape.

Cuticular layers with indistinct epidermal cells of rectangular to polyonal shape; stomata anomocytic, indistinct, hairs present, both layers have *Heliospermopsis darrangei* Banerjee (1991, 1995) type salt glands with irregular distribution pattern; frequency is 16–18/mm^2 (Fig. 2).

Cuticular layers of both *S. acuminatum* and *D. ellipticum* are crowded with epiphyllous fungi viz., *Meliolinites spinksii* (Dilcher) Selkirk, *Callimothallus pertusus* Dilcher, *Haplopeltis mucoris* Dilcher, *H. bhutanensis* Banerjee (1991, 1995), *H. lakshmii* Banerjee (1991, 1995). The fungal assemblage on the cuticles of the angiosperm leaves from Siwalik sediments of Bhutan suggest tropical, subtropical climate and a high rate of precipitation.

Angiosperm palynofloristics in the Siwalik sediments of Bhutan

Palynoassemblages recovered from Lower, Middle and Upper Siwalik sediments of four river traverse viz., Darranga, Jiabar, Kalapani and Lakshmi rivers (Fig. 1) of Bhutan, Eastern Himalaya, are rich in palynoflora (Das Gupta, 1991; Banerjee & Das Gupta, 1995) compared to palynoassemblages of other Siwalik sectors (Mathur, 1984). Angiosperm pollen grains are represented in the palynoassemblage of Bhutan by more than fifty percent. Out of 169 species of total mioflora recovered under 101 genera, 88 species under 57 genera belong to angiosperm. Twenty five species of monocotyledonous pollen grains under 12 genera and 45 genera of dicotyledonous pollen grains with 63 species are identified. Distribution pattern of the monocotyledonous and dicotyledonous pollen grains in the Siwalik succession, botanical affinity and environment are detailed in Table 2.

Table 2

(LS = Lower Siwalik; MS = Middle Siwalik; US = Upper Siwalik)

Angiosperm taxa	Horizon	Botanical affinity	Environment
Monocotyledons			
1. *Retipilonapites*	MS	Potamogetonaceae	Aquatic, Cosmopolitan
2. *Verruinaperturites*		,,	Aquatic, Cosmopolitan (fresh or somewhat brackish water)
3. *Rusizia*		Cannaceae/Zingiberaceae	Tropical and Subtropical
4. *Palmaepollenites*	LS, MS, US	Arecaceae	Tropical and Subtropical, Coastal
5. *Palmidites*	MS	,,	,,
6. *Arecipites*	LS, MS	*Phoenix* (Arecaceae)	Tropical and temperate
7. *Liliacidites*	LS, MS	Liliaceae	Tropical to warm temperate
8. *Proxapertites*	LS, MS, US	Arecaceae	Tropical, Subtropical and Coastal
9. *Spinizonocolpites*	MS	*Nypa* sp. (Arecaceae)	,,
10. *Dicolpopollis*	LS, MS, US	*Calamus* sp. (Arecaceae)	,,
11. *Graminidites*	US	Poaceae	Cosmopolitan
12. *Sparganiaceaepollenites*	US	Sparganiceae	Aquatic, Temperate
Dicotyledons			
1. *Bombacacipites*	MS	*Freemontodendron* sp. (Sterculiaceae)	Pantropical and Subtropical
2. *Cupuliferoidaepollenites*	MS	Uncertain	Temperate
3. *Ranunculacidites*	MS	Ranunculaceae	Cosmopolitan
4. *Retitrescolpites*	MS	*Cuscuta* sp. (Convolvulaceae)	Tropical and Temperate
5. *Retitricolpites*	MS	Uncertain	
6. *Salixipollenites*	MS	*Salix* sp. (Salicaceae)	Temperate and Cosmopolitan

Angiosperm taxa	Horizon	Botanical affinity	Environment
7. *Tricolpites*	LS, MS, US	Uncertain	
8. *Quercoidites*	MS	(?) Tiliaceae	Tropical and Temperate
9. *Polycolpites*	MS	Polygalaceac	Cosmopolitan
10. *Retistephanocolpites*	MS	Ctenolophonaceae	Cosmopolitan
11. *Araliaceoipollenites*	MS	Araliaceae	Tropical
12. *Caprifoliipites*	MS	Caprifoliaceae	,,
13. *Cupuliferoipollenites*	LS, MS	Cupuliferae	Temperate
14. *Favitricolporites*	MS	Uncertain	
15. *Foveotricolporties*	MS	*Nyssa* sp. (Nyssaceae)	Tropical and Temperate
16. *Horniella*	MS	Rutaceae	Tropical and Temperate
17. *Rhoipites*	MS	Anacardiaceae	,,
18. *Bombacacidites*	MS	*Salmolia albuni* (Bombacaceae)	Tropical
19. *Compositoipollenites*	MS	Asteraceae	Cosmopolitan
20. *Striacolporites*	MS	Uncertain	
21. *Margocolporites*	MS	Caesalpiniaceae	Tropical and Subtropical
22. *Palaeocoprosmadites*	MS	*Coprosma* sp. (Rubiaceae)	,,
23. *Pellicieroipollis*	MS	Theaceae	,,
24. *Polygalacidites*	MS	Polygalaceae	Cosmopolitan
25. *Sapotaceoidaepollenites*	LS, MS	Sapotaceae	Tropical
26. *Nymphaeacidites*	MS	Nymphaeaceae	Aquatic, Cosmopolitan
27. *Annutriporites*	MS	Uncertain	
28. *Engelhardtioidites*	LS, MS	Juglandaceae	Temperate
29. *Malvacearumpollis*	MS, US	Malvaceae	Tropical
30. *Myricaceoipollenites*	MS, US	Myricaceae	Temperate
31. *Myrtaceidites*	MS	Myrtaceae	Tropical
32. *Retitriporites*	MS	Uncertain	
33. *Tiliaepollenites*	MS	Tiliaceae	Tropical
34. *Triporopollenites*	MS	Betulaceae/Myricaceae	Temperate
35. *Caryapollenites*	LS, MS	*Carya* sp. (Juglandaceae)	Temperate
36. *Subtriporopollis*	MS	Uncertain	
37. *Alnipollenites*	MS, US	*Alnus* sp. (Betulaceae)	Temperate
38. *Haloragacidites*	MS	Haloragaceae	Cosmopolitan
39. *Pterocaryapollenites*	MS, US	*Pterocarya* sp. (Juglandaceae)	Temperate
40. *Caryophyllidites*	LS, MS	Caryophyllaceae	Cosmopolitan
41. *Chenopodipollis*	US	Chenopodiaceae	,,
42. *Juglanspollenites*	MS	Juglandaceae	Temperate
43. *Droseridites*	MS	Droseraceae	Cosmopolitan
44. *Polyadopollenites*	MS, US	Uncertain	
45. *Palaeosantalaceaepites*	MS	Rhizophoraceae	Tropical, Mangrove

Angiosperm floristics and environment of Siwalik sediments of Bhutan

Environment analysis of the megaplant angiosperms (Table 1) and angiosperm palynofossils (Table 2), distribution pattern of the taxa in the stratigraphic succession reveal a predominantly tropical-subtropical, humid environment of deposition of the Bhutan Siwalik sediments. The flora initiated with a mild coastal influence during Lower Siwalik as is revealed from the occurrence of *Palmaepollenites, Proxapertites,* etc. During Middle Siwalik maximum diversity of angiosperm vegetation occurred in the area including a phase of estuarine environment. Occurrence of *Palmaepollenites, Proxapertites, Spinizonocolpites, Dicolpopollis,* pollem grains cf. Rhizophoraceae, viz., *Palaeosantalaceaepites* spp. and the mangrove leaf *Avecinnia, Aegiceras* like angiosperms in the Middle Siwalik suggest the occurrence of mangrove swamp in the area. The intensity of marine influence, however receded in the Upper Siwalik. Temperate climate angiosperm plant pollen are not very diverse in the Middle or Upper Siwalik as in the Siwalik sectors of Western Himalaya (Mathur, 1984). Records of some temperate climate plant pollen gains viz., *Sparganiaceaepollenites, Triporopollenites, Caryapollenites, Alnipollenites, Pterocaryapollenites, Juglanspollenites* in the Middle and Upper Siwaliks suggest that highland topography existed in near vicinity at the time of deposition of the foreland basins. Palynofloristic zones proposed (Banerjee & Das Gupta, 1995) for the Siwalik sediments of Bhutan (Table 3) and the environment analysis of the flora (Banerjee, 1991, 1995) including angiosperms (Fig. 3) also suggest a tropical-subtropical, humid climate with coastal to estuarine marine to coastal environment in the Neogene sediments of Bhutan.

A comparative analysis of the Neogene angiosperm vegetation with the modern floristic pattern suggest that the area was more towards lower latitude during Neogene and enjoying tropical climate, higher rate of precipitation and marine inundation. The orogenic movement of Himalayan upliftment gradually changed the palaeogeography of the marine inundated Siwalik basin to a highland mountaninous topography in Bhutan. Some of the angiosperm families particularly those of temperate climate of modern vegetation of Bhutan, however, is surviving for a long time in the area for about 10 million years.

Angiosperm floristics of the Siwalik basins of Indian subcontinent

A large number of plant megafossils and palynofossils are recorded from each of the sectors of Siwalik foreland basins of Indian subcontinent which have been briefly reviewed by Singh (1992) and Mathur (1984). To add a few more records not included in the reviews are plant megafossils from Darjeeling foothills (Pathak, 1969; Antal & Awasthi, 1993), Bhutan (Banerjee & Das Gupta, 1984; Banerjee, 1984; 1985, 1991, 1995), Nepal and Bihar (Prasad, 1990a, 1990b, 1994a; Srivastava et al., 1992a, 1992b) and Uttar Pradesh (Prasad, 1994b). Plant megafossils of tropical subtropical, humid climates are recorded from all the sectors. No plant megafossils of cool climate are yet recorded from the Siwalik sediments indicating the environment of deposition of Siwalik foreland basins as predominantly tropical subtropical.

Palynofossils however are represented by tropical, subtropical, temperate cool climate plants. In addition to the records of mangrove plants of estuarine habitat in the upper part of

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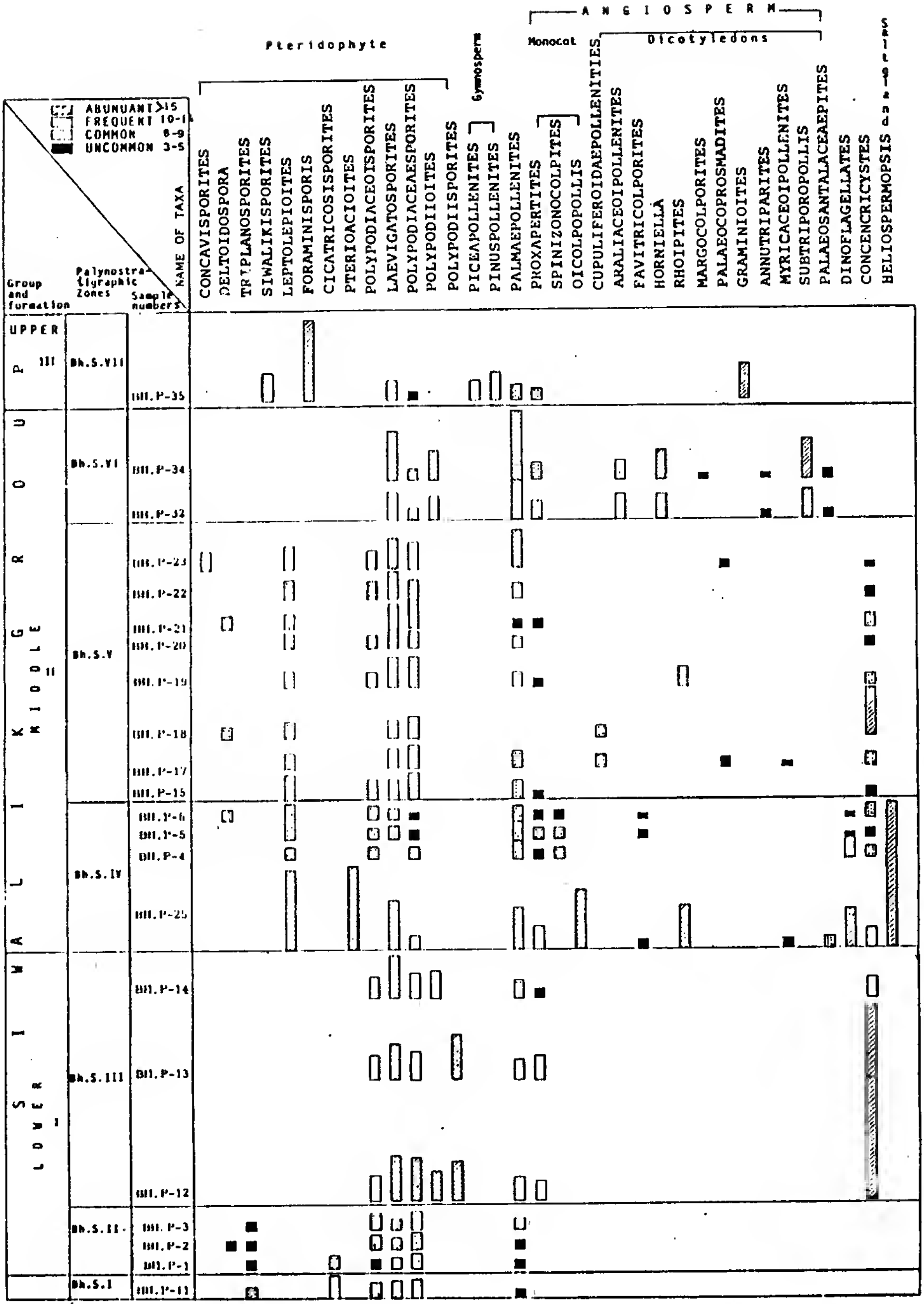

Table 3. Relative frequency of occurrence of Angiosperms in the Palynostratigraphic Zones recorded from Siwalik sediments of Bhutan, Eastern Himalaya.

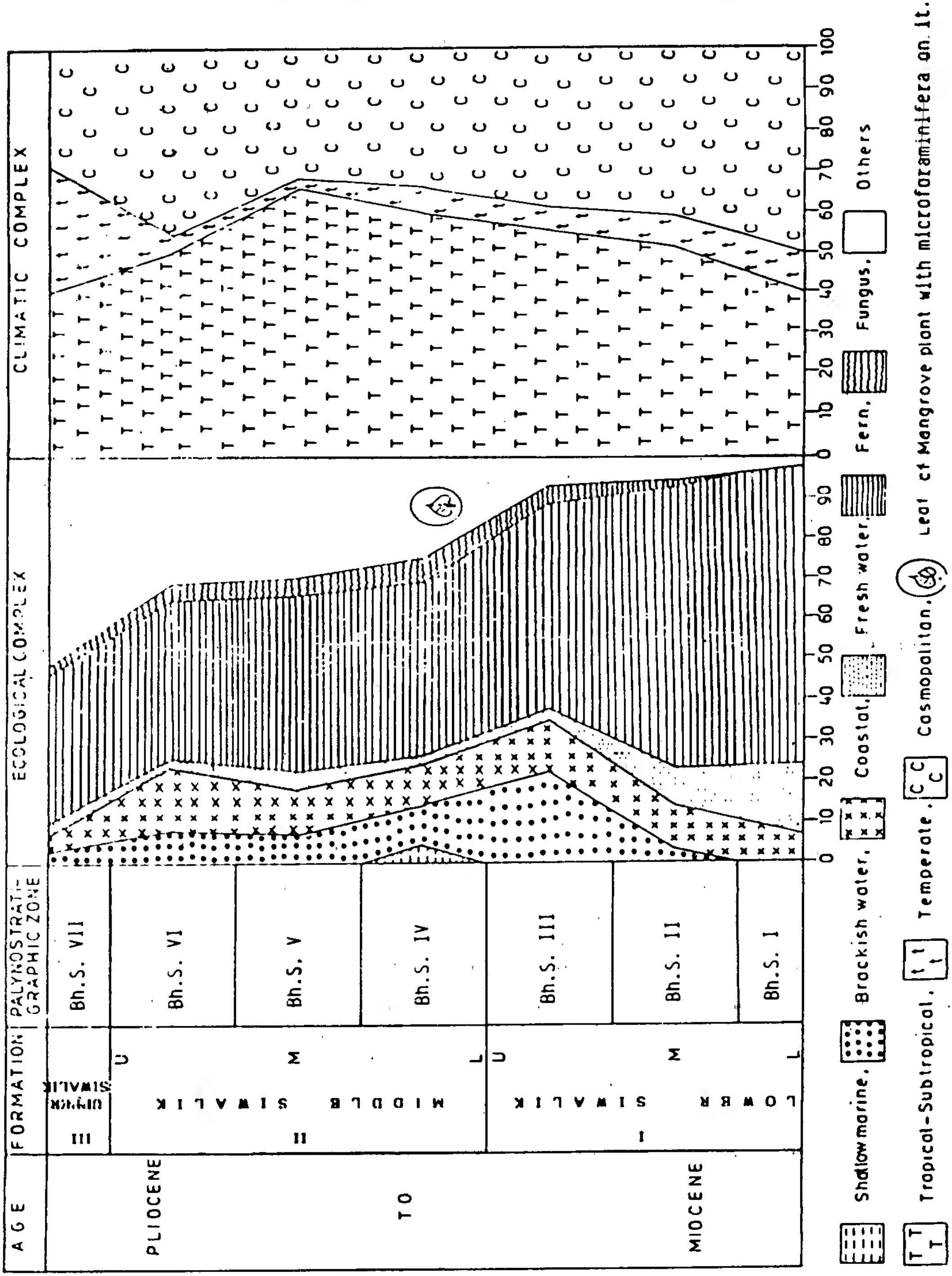

Fig. 3. Environmental complex analysis of the palynostratigraphic zones and angiosperm plant remains recorded in the Siwalik sediments of Bhutan, Eastern Himalaya.

Lower and lower part of Middle Siwalik of Bhutan, Darjeeling foothills (Banerjee, 1984, 1985, 1995), pollen grains of mangrove plant affinity, viz., *Zonocostites, Florschuetzia* are recorded from the upper part of Lower Siwalik of Himachal Pradesh. Besides, microplanktons are also recorded from this horizon of Himachal Pradesh Siwalik sector and Ganga Valley of Uttar Pradesh.

The temperate climate pollen in the western sector basins appear to have been produced by the plants of nearby highland mountains. More diversity and frequency of such pollen in the palynoassemblages of Lower, Middle and Upper Siwaliks suggest an early and more intense orgogenic activities in the western Himalaya to form high mountains in the vicinity of Siwalik basins.

Angiosperm floristics of Siwalik foreland basins reveal that the areas were in lower latitude tropical climate, high rainfall zone; moreover, Bhutan, Darjeeling foothills, Himachal Pradesh, Ganga Valley sectors were nearer to sea shore where marine inundation influenced the vegetation during upper part of Lower Siwalik to lower part of Middle Siwalik. Highland topography emerged due to Himalayan orogeny during Siwalik sedimentation.

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